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STUDIES UPON THE BIOLOGICAL SIGNIFICANCE OF ANIMAL COLORATION

II. A REVISED WORKING HYPOTHESIS OF MIMICRY

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ALTHOUGH zoologists know that detailed resemblance in outward appearance may occur between different species of insects which are not closely related, they do not agree in their interpretation of the facts they observe. Present knowledge, indeed, justifies nothing more than tentative explanations of mimicry; but, in this matter, observations recently reported[1] limit one's freedom of choice, since they appear to bear directly upon the validity of current hypotheses reviewed in the following pages.

The first attempt to interpret mimetic resemblance as a result of natural selection was made by H. W. Bates,[2] who writes:

> What advantage the Heliconidæ possess to make them so flourishing a group, and consequently the objects of so much mimetic resemblance, it is not easy to discover. . . . It is probable that they are unpalatable to insect enemies. . . . They have all a peculiar smell. I never saw flocks of the slow flying Heliconidæ in the woods persecuted by birds or dragon flies, to which they would have been an easy prey;

[1] Longley, "The Colors and Color Changes of West Indian Reef-fishes," *Jour. Exp. Zool.*, 1917. It happens that the present paper will appear slightly before that cited.

[2] *Trans. Linn. Soc. Lond.*, Vol. 23, p. 510.

nor, when at rest on leaves, did they appear to be molested by lizards or the predaceous flies of the family Asilidæ, which were very often seen pouncing on butterflies of other families. If they owe their flourishing existence to this cause, it would be intelligible why the Leptalidæ, whose scanty number of individuals reveals a less protected condition, should be disguised in their dress, and thus share their immunity.

Bates himself points out the fact that "some of the mutual resemblances of the Heliconidæ seem not to be due to the adaptation of the one to the other, but rather, as they have a real affinity, . . . to the similar adaptation of all to the same local, probably inorganic conditions." Thus the application of his hypothesis was limited from the beginning.

Fritz Müller[3] showed how those instances of resemblance which his predecessor ascribed to the influence of Lamarckian factors might be aligned with the Darwinian hypothesis. In Meldola's[4] translation of his original paper his idea is expressed as follows:

What benefit can one species derive from resembling another, if each is protected by distastefulness? Obviously none at all, if insectivorous birds, lizards, etc., have acquired by inheritance a knowledge of the species which are tasteful or distasteful to them—if an unconscious intelligence tells them what they can safely devour and what they must avoid. But if each single bird has to learn this distinction by experience, a certain number of distasteful butterflies must also fall victims to the inexperience of the young enemies. Now if two distasteful species are sufficiently alike to be mistaken for one another, the experience acquired at the expense of one will likewise benefit the other; both species together will only have to contribute the same number of victims which each of them would have to furnish if they were different.

Recent years have been marked by a tendency upon the part of some observers[5] to extend the bounds of the Müllerian associations, until in a given fauna a large proportion of the insects which show the same color combination are included in one bionomic group. Scores of species have, indeed, been assigned to some, and it has

3 *Kosmos*, May, 1879, p. 100.

4 *Proc. Ent. Soc. Lond.*, 1879, p. xxvii.

5 Marshall and Poulton, "The Bionomics of South African Insects," *Trans. Ent. Soc. Lond.*, Vol. 41, pp. 287–584.

been alleged that very many types from the same region show the influence of one or another of the dominant Müllerian aggregations. Müller's hypothesis, however, has not attained preeminence solely by extension to newly discovered cases of resemblance, but has prospered in many instances at the direct expense of the Batesian conception. Its changed fortune depends largely upon Dixey's[6] discovery of mimetic attraction, or reciprocal mimicry.

This relation, which it is held exists between many insects previously considered typical Batesian couples, suggests that the observed resemblance involves mutual adjustment. But the idea that each species introduces into its own pattern elements characterizing that of the other, and thus contributes actively to the development of a common type of coloration, is intelligible in terms of the mimicry hypotheses, only if the superficial resemblance so attained is mutually advantageous. Whatever justifies change in the interpretation of fact lies here; for, if it be assumed in the beginning that the likeness noted must have arisen either through the action of Batesian or Müllerian factors, it must be admitted that the notion of mutual advantage seems more fitly associated with the latter: two species, each of which enjoys marked immunity, seem better able to force reciprocal concessions in their achievement of resemblance, than they should, if there were great disparity in their means of defence.

Perhaps the most obvious suggestion from Dixey's research is not, after all, that a closer approximation to truth may possibly be attained through reclassification of mimetic resemblances, but that an intergrading series of alleged Batesian and Müllerian mimics is perfectly conceivable, in which no known test could possibly determine the occurrence of a natural break. Hence there would seem to be only historical reasons for maintaining the two categories.

It is noteworthy that neither hypothesis to which reference has been made was in its original form an attempt

[6] *Trans. Ent. Soc. Lond.*, 1894, pp. 249–334.

to explain the existence of conspicuous creatures. The sole concern of each was the interpretation of resemblances, which were later commonly considered mere incidents in the attainment and use of warning colors. This shifting of emphasis from "likeness which is perfectly staggering"[7] to conspicuousness, which failed to elicit a single outspoken comment in the original papers of Bates and Müller, is distinctly chargeable to Wallace,[8] who extended his hypothesis of the functional conspicuousness of bright colors, until it included the facts of mimicry.

Abbott H. Thayer[9] has proposed an explanation of the resemblance between unrelated species of butterflies, which is consistent with his thesis that the foremost function of animal coloration is concealment. This hypothesis is Darwinian in principle, but in practise is directly opposed to current selectionist opinion. It is purely speculative, and is stated as follows:

> It is surely conceivable that in a certain region, one particular form of flower-scenery representation may furnish such advantage to butterflies as to cause many widely separated species to become modified till they wear a common aspect, and it is conceivable also that there would be one common form of wing that would best lend itself to this scheme.

More recently Thayer[10] adds that in the paper from which the excerpt above is taken he ascribed more importance to butterflies' resemblance to flowers, as compared to their rendering of scenery, than he should at the later date; but this necessitates no modification of his idea that mimicry is mere incidental resemblance between species, which, through selection based upon the obliterative effect of their coloration, conform ever more closely to one ideal representation of their common background.

If the Darwinian ranks are divided upon the question of the prevalence of conspicuous types of coloration, similar though less open dissension appears among their op-

[7] Bates, *l. c.*, p. 507.

[8] Darwinism, p. 239. Macmillan and Co., 1891.

[9] *Trans. Ent. Soc. Lond.*, Vol. 42, p. 557.

[10] See Thayer, Gerald H., "Concealing Coloration in the Animal Kingdom," Appendix *B*, p. 251. Macmillan and Co., 1909.

ponents. To Piepers,[11] for example, specific coloration is in large part a visible token of internal organization determined from time immemorial, a result of orthogenetic evolution capable, however, of being accelerated or retarded by external conditions. To Packard[12] it represented a racial response of organism to environment, and mimicry seemed an effect of exposure to conditions of the same kind. But if evolutionary processes be largely beyond the control of external agents, and species spring from species through internal reorganization, as one configuration follows another in the kaleidoscope, one should anticipate that many color combinations of exaggerated conspicuousness might result. If, upon the other hand, the development of color and pattern be determined by animals' environment, their coloration may well repeat dominant notes from their surroundings. Hence it is not surprising to find that Packard expresses hearty appreciation of Thayer's discoveries, and Piepers, despite his anti-Darwinian attitude, might have much in common with Wallace and Poulton. Thus the full series of contradictions is rounded out, and the unsettled state of opinion concerning mimicry, or indeed the whole matter of animal coloration, is apparent, for the two qualities, utility and conspicuousness, openly or tacitly affirmed or denied, may be ascribed in every possible combination to the color and pattern of a single organism.

It may apparently be stated safely without qualification that the bright colors of tropical fishes as a class are correlated with the animals' habits, and, in the case of all but red, distinctly repeat tones characterizing their normal environment. But, other things being equal, no one will maintain that any system of external pigmentation could be less conspicuous than one conforming to this principle. Therefore, among these creatures at least, the occurrence of bright colors in contrastive patterns is not inconsistent with the idea that the forms that display them are as inconspicuous as may be under the conditions in which they

[11] "Mimikry, Selektion und Darwinismus." Leiden, 1903.

[12] *Proc. Amer. Philos. Soc.*, Vol. 43, p. 421.

live. It is this fact that necessitates a review of hypotheses of animal coloration that postulate conspicuousness; for one cannot safely disregard the suggestion that principles applicable to one group of animals may be valid also in the case of others.

It is of interest to note that Chapman[13] studied the birds of Trinidad under favorable conditions and observed that distinct types of coloration marked those of different habits. The most brilliant species occupy the most exposed positions in the treetops. More sedentary forms inhabiting the body of the trees are largely green, and brown predominates in the coloring of those that climb upon the tree-trunks, frequent the undergrowth near the forest border, or live upon the forest bottom.

These ecological records are a mere incident, a by-product of their author's activity. Through lack of detail they possess no great intrinsic value, but are highly significant in their present setting. Mention should also be made of Potts'[14] observation that shrimps living symbiotically with crinoids upon the Australian reefs repeat the colors of the forms with which they are associated. That comparable facts regarding other groups of animals are not available is immaterial. If the bright colors of tropical birds, fishes and some crustacea repeat those of the animals' respective environments and minister to the inconspicuousness of their possessors, it is of interest to inquire what data and reasoning support the contention that in insects similar combinations bear a different relation to the colors about them and discharge another function.

It appears first, from the statements of a number of their more prominent advocates, that there are fundamental theoretical objections to the hypotheses of warning coloration and mimicry.

Poulton[15] remarks that the acquisition of an unpleasant taste or smell, together with a conspicuous appear-

[13] *Bull. Amer. Mus. Nat. Hist.*, Vol. 6, pp. 19–20.

[14] Carn. Inst. Wash., *Papers Dept. Mar. Biol.*, Vol. 9, pp. 71–96.

[15] *Proc. Zool. Soc. Lond.*, 1887, p. 192.

ance, is so simple a form of protection, and yet *ex hypothesi* so absolutely complete, that it seems remarkable that more species have not availed themselves of this mode of defence. He argues that if once their potential vertebrate enemies were driven to eat any such insects in spite of their unpleasant taste, they would almost certainly soon acquire a relish for what was previously disagreeable, and the insects would be in great danger of extermination, having in the meantime become conspicuous by gaining warning colors. He concludes that if this reasoning is correct, it is clear that this mode of defence is not necessarily perfect, and that it depends for its apparently complete success upon the existence of relatively abundant palatable forms: in other words, its employment must be strictly limited.

Dixey[16] encounters the same difficulty in his consideration of Batesian mimicry. He observes that in this relation the advantage is all on the side of the edible mimicking species, whose existence is, indeed, a source of danger to the form mimicked, inasmuch as any experience gained by tasting the former would be used to the detriment of the latter. From these considerations he believes that such an association can exist only when the numbers of the one species are insignificant in comparison with those of the other. Upon this point he is in essential agreement with Wallace,[17] who states that mimicry has been shown to be useful only to those species and groups that are rare and probably dying out, and would cease to have any effect should the proportionate abundance of mimic and model be reversed.

Here, then, are two hypothetical types of association whose persistence admittedly depends upon the maintenance of definite though undetermined ratios between their components. Hence it devolves upon those who hold that the assumed relations are real, to outline some system by which the due proportion of protected and unpro-

[16] *Trans. Ent. Soc. Lond.*, 1897, pp. 317–332.
[17] *Westminster Review*, Vol. 32, N. S., p. 35.

tected forms might be maintained through the interaction of natural factors.

In an attempt to avoid this preliminary difficulty Poulton declares that it has always been recognized that an insect may be distasteful to one vertebrate enemy, but palatable to another. He suggests a different counterbalancing limit, which he admits would certainly in time become identical with the other. He argues that a vertebrate enemy may be forced by stress of hunger to eat an unpalatable insect, by implication asserts that this adaptability of potential enemies of forms tending to assume warning colors would limit the number of species developing them, and considers the truth of his suggestion confirmed by experimental tests.

It seems, however, that as long as warning coloration confers any advantage, other species should move in the same direction, for the same reasons that those did in which it first appeared. The number of warningly colored species should therefore increase until the situation conceived by Poulton materialized. But in that event the experimental proof that hungry animals are not so fastidious as those that are well fed is insufficient to meet the exigencies of the situation; for one has no reason to believe that animals which might become adjusted to the new condition would confine themselves to a diet of insects whose warning coloration was recently acquired, and would leave intact the vested interests of those that first attained it. Indeed, if one is permitted to speculate, it seems not wholly unreasonable to anticipate a swing of the pendulum in the other direction, so that conspicuous forms might face the possibility of almost complete extinction. This is suggested by the well-known fact that interspecific adjustments are not rigid, and that a state of approximate equilibrium is frequently modified by climatic or other factors, and restored only after a series of more or less definite oscillations. Examples in point are furnished by Howard's[18] observations upon ichneu-

[18] "New Nature Library," Vol. 7, Pt. 1 (The Insect Book), p. 68. New York, Doubleday, Page and Co.

mon flies and their primary and secondary parasites, and more particularly by those of Forbes[19] and Bryant[20] upon the feeding habits of birds.

In his paper, which has been cited above, Dixey was not discussing the validity of the mimicry hypotheses and has not attempted to explain what limits the numbers of a mimic in proportion to those of its model. Wallace also failed to elucidate the mystery, leaving his readers to find the way out of their difficulty as they might best be able. Search elsewhere for helpful suggestion in the matter yields little of value. Poulton[21] holds that ichneumon flies are particular enemies of the larvæ of "protected" Lepidoptera, but this idea need not be taken very seriously at present, for it is apparently based upon the observation of a high proportion of parasitized individuals among such forms rather than upon comparative statistics covering "unprotected" species as well. Even if it were true, while it would bolster the warning color hypothesis, it would aggravate the situation regarding Batesian mimicry. Therefore only one conclusion is possible: The theoretical objections they themselves have raised are not adequately met by spokesmen for the two hypotheses.

What observed facts support the contention that many animals are made conspicuous and profit by the striking combinations of color they display, should next be determined.

In 1867 Wallace[22] suggested before the Entomological Society of London that, as a rule, brilliantly colored larvæ are distasteful to birds, expressed his desire for information and his gratification, if any who kept birds, particularly indigenous species, would make experiments with different larvæ to ascertain which were eaten and which rejected. Members of the society and others have repeatedly acted upon his suggestion and commonly

19 "The Regulative Action of Birds upon Insect Oscillation," *Ill. State Lab. Nat. Hist.*, Bull. No. 6.

20 "The Condor," Vol. 13, 1911, pp. 195–208.

21 "The Colors of Animals," p. 182. New York, D. Appleton and Co., 1892. For additional data, see *Trans. Ent. Soc. Lond.*, Vol. 41, p. 337.

22 *Proc. Ent. Soc. Lond.*, 1867, pp. lxxx–lxxxi.

agree that the results of the experiments support his hypothesis, whose application has meanwhile been greatly extended. But the spirit in which the observed facts are interpreted precludes all possibility of the main inference drawn from them being seriously considered by any unprejudiced critic who examines the argument.

If a dull-colored insect be eaten, this is held by implication to lend strong support to the hypothesis of warning coloration; for palatable insects must be inconspicuous or be destroyed. If, upon the contrary, such an insect be rejected, its distastefulness may be a useless character, an accident of metabolism, or vestigial, or may be related to functional distastefulness in preceding stages of the life history; in any case "it must be remembered that an unpleasant attribute must always appear in advance of the warning coloring,"[23] so the result is not inconsistent with Wallace's suggestion. Again, if a bright-colored insect be rejected, this accords with his contention; and finally, if such a one be accepted, experimenters are prone to agree with J. Jenner Weir[24] who writes:

> But I am by no means inclined to attach undue importance to this fact, because the birds, being in a state of confinement, might readily be expected to eat insects, which in a state of nature, with a less limited choice, they would reject.

It is unnecessary to review these experiments in detail and to attempt to evaluate them, for this has already been done thoroughly by McAtee,[25] who shows their utter futility by comparing typical observations upon caged birds with the facts revealed by analysis of the stomach contents of wild specimens of the species experimented upon. Regarding information from such sources as that last-mentioned he writes:

> Since this evidence is sufficient in itself and since experimental data must be supported by it, why perform the experiments? The same time spent in collecting trustworthy data regarding the natural food

[23] Poulton, "The Colors of Animals," p. 176.

[24] *Trans. Ent. Soc. Lond.*, Vol. 7, Ser. 3, p. 22.

[25] *Proc. Acad. Nat. Sci. Phila.*, 1912, pp. 281–364.

habits of animals would bring much greater returns, and the result would be truth, not imaginative inferences from abnormal behavior.

Before concluding the discussion of this matter it should be stated that even if it were proved that bright-colored insects are distasteful, it might not be inferred fairly that they are conspicuous, or that their coloration has a specific warning (aposematic) function. Feeding experiments under ideal conditions might determine the presence or absence of distastefulness, and show to what extent it is correlated with the display of color combinations of a particular sort. But even a high degree of correlation between unpalatability and gaudy coloration proves that the latter is conspicuous, no more than the demonstration that an unknown substance has the approximate *hardness* of gold proves that it has the same *specific gravity;* for brightness, or vividness of coloration, and conspicuousness are incommensurable.

Except in Thayer's contributions, confusion upon this point has prevailed from the beginning, when Wallace used interchangeably the expressions, "brilliantly colored larvæ" and "caterpillars conspicuous by their lively coloration." But the assumption that some animals are conspicuous, or, in other words, that while their habits remain the same their average visibility might be greatly diminished by another system of coloration than that they possess, can neither be adequately defended nor refuted, until the results of such exhaustive studies of animals' habits as have rarely been attempted are available. The distribution of animals must be studied intensively, for the division of the world into provinces and the subdivision of these into their major components by gross dissection is not a technique of sufficient refinement to discover the essential relations between organism and environment.

Passing to another phase of the matter, the value of recorded observations upon the conspicuousness of insects may be shown very clearly.

Bates saw no Heliconidæ attacked by dragonflies or

other predaceous insects which often pounced upon butterflies of other families. But Poulton[26] finds, to state it mildly, that "there is good reason for believing that such attacks are not rarely made, and that predaceous insects are important enemies of aposematic butterflies." He also writes[27] of the Batesian hypothesis:

> This was not, as has been generally supposed, originated by Bates during his years of observation in the Valley of the Amazon. It arose in his mind after his return home, when he came to examine his collection and to reflect upon his experiences.

Under these circumstances the uncorroborated testimony of this witness concerning matters which are not known to have been carefully investigated in the Brazilian wilderness and are not determinable from the study of preserved material is of little immediate consequence. Among subjects regarding which his opinion can at present be held only in slight esteem, and concerning which he expressed himself in other communications than his original paper upon mimicry, the inherent conspicuousness of bright colors may be justly included.

The positive assertions in the following quotation describing conditions observed by an entomologist in British Guiana are also instructive; the same is true of their author's naïve conclusion.

W. J. Kaye[28] writes:

> The forest is dark and gloomy, and throughout the greater part of the year excessively damp owing to a superabundant rainfall. The character of the vegetation is always the same, as even in the dry season the trees are never otherwise than a fresh green. It is not surprising, therefore, that practically the whole of the Lepidoptera, excepting, of course, the several species of *Morpho*, present a very uniform, somber tone of coloration. Even the very fine and brightly colored *Heliconius catharinæ*, *H. astydamia* and *H. egeria* do not strike one in their surroundings as being particularly gaudy, and one is bound largely to admit the assertion of Abbott H. Thayer that many species we call conspicuous are not really so in their natural surroundings. It must, however, have been quite impossible for nature to have evolved such

[26] *Trans. Ent. Soc. Lond.*, Vol. 41, p. 328. See also Vol. 44, pp. 323–409.

[27] "Essays on Evolution," p. 211. Oxford, Clarendon press, 1908.

[28] *Trans. Ent. Soc. Lond.*, Vol. 44, p. 412.

minutely close resemblance in unrelated groups without the aid of Müllerian mimicry.

It remains to state that among Lepidoptera different species have their characteristic attitudes of rest, frequent different places, fly at different levels, and are active at different times in the day. Even the two sexes of some species, and these are commonly dimorphic forms, do not haunt the same stations. It is certainly a pregnant fact, which we may accept since Wallace[29] gives independent testimony to the same effect, that Bates[30] observed many, apparently scores, of species, in which, as he says, the sun-loving males flaunted their gaudy hues in open places, while their respective females, soberly clad, frequented the forest shades.

These facts and others that might be cited are indications of diversity of habit among insects comparable with that which among fishes is correlated with the display of different types of inconspicuous coloration. They suggest that in this group as well, external pigments are distributed among species according to an intelligible system other than that whose existence is commonly inferred. But if this should eventually prove to be true, we must have an explanation of mimicry without appeal to the concept of warning colors.

Such a hypothesis has in fact been formulated by Punnett,[31] for in spite of his apparent belief in the conspicuousness of many species of butterflies it happens that he lays no stress upon it in his consideration of the origin of mimetic resemblance. His hypothesis, as he fully recognizes, is at present little more than naked suggestion. It is ingenious, is stated attractively in the current idiom of genetics, and is effectively displayed against a background of destructive criticism of its predecessors, from which it differs in minimizing the influence of nat-

[29] *Trans. Ent. Soc. Lond.*, Vol. 2, Ser. 2, pp. 253–264.

[30] "The Naturalist on the River Amazon," p. 291. Reprinted, New York, D. Appleton and Co., 1892.

[31] "Mimicry in Butterflies." Cambridge, University Press, 1915.

ural selection. It proposes an entirely new explanation of mimicry in the following terms:

> If we assume that sudden and readily appreciable variations of the nature of "sports" turn up from time to time, and if these variations happen to resemble a form protected by distastefulness so closely that the two can be confused by an enemy which has learned to avoid the latter, then there would appear to be good grounds for the mimicking sport becoming established as the type form of the species. . . . On this view natural selection in the form of the discriminating enemy will have played its part, but now with a difference. Instead of building up a mimetic likeness bit by bit it will merely have conserved and rendered numerically preponderant a likeness which had turned up quite independently. . . . Why variations on the part of one species should bear a strong resemblance to other, and often distantly related, species is another question. . . . The occurrence of mimetic resemblances is the expression of the fact that color pattern is dependent upon definite hereditary factors of which the total number is by no means very great. As many of the factors are common to various groups of butterflies, it is to be expected that certain of the color patterns exhibited by one group should be paralleled by certain of those found in another.

Upon examination these statements appear to embody a formal explanation of the facts to which it is difficult to take exception. Hence it must be admitted that this is perhaps the goal toward which with regard to this problem naturalists have been working for more than half a century. But while his hypothesis may be correct, its author's reasons for deeming it so seem quite insufficient.

The chief points of support on which it rests are the following, which are not arranged in the order of importance assigned to them:

1. The difficulty of finding the appropriate enemy which shall exercise the discrimination postulated by current hypotheses.

2. The alleged fact, mathematically demonstrated, that reciprocal mimicry between two species can not be established by selection of a long series of slight variations.

3. The theoretical difficulty of the initial variation in cases other than that above, for it seems reasonable that if the ancestral types from which mimic and model are derived were in the beginning very unlike in appearance

no slight departure from one in the direction of the other could have selective value.

4. The non-appearance of intermediates when a form which is assumed to have been derived from another by selection of a series of heritable variations (mutations) is crossed back with the original.

5. The apparent fact that the three females of the polymorphic oriental butterfly, *Papilio polytes,* occur in proportions which are approximately the same now as fifty, or possibly one hundred and fifty years ago, although it may be demonstrated mathematically that if either of the two mimetic forms possesses even a slight advantage over that from which they are assumed to be descended, this should have appeared in an altered ratio while they continue to live and breed together under the same conditions.

6. The fact that certain variations induced by differences in temperature or humidity are not directly inherited, since it is alleged that this limits the material upon which selection might be supposed to operate.

Of these points the first three may be more conveniently considered later with other common objections to current hypotheses of mimicry. The remaining three will be next examined in order.

Punnett accepts Fryer's[32] conclusion that in *P. polytes* the two supernumerary females which resemble *P. aristolochiæ* and *P. hector* differ genetically from the third female (which resembles the male) to the extent of one and two Mendelian factors, respectively. He cites the fact that there are forms of sweet peas, for example, which are known to have arisen as sudden sports, and behave in heredity as though they differed from the normal by a single factor. Hence he infers from analogy, first, that the two mimetic butterflies sprang from the primitive type by one or two mutations, as the case may be, and, as a corollary, that resemblance to their models was not attained by gradual shaping of their destinies

[32] *Phil. Trans. Roy. Soc. Lond.,* Vol. 204 *B.*

through the accumulation of lesser variations by natural selection.

But Castle[33] still contends vigorously that a single genetic character may undergo quantitative change under selection, and if this be true the difference finally attained by two forms differing only in one factor might follow from the accumulation of an indefinite number of slight variations. Still the complete abandonment of Castle's position would not save Punnett's argument. For if reported observations and inferences concerning *Drosophila*[34] are correct, a red-eyed strain has given rise to white by mutation and this in turn to eosin, which being crossed with the original red gave in the F_2 generation offspring in the proportion of three red to one eosin.

It is quite immaterial whether one explains these relations upon the hypothesis of multiple allelomorphs, or, as Punnett[35] prefers, upon the assumption of complete coupling of factors. In the former case one must admit that by breeding experiments the end product of a series of mutations can not be indubitably distinguished from one that results from a single modification of the affected factor. In the latter, one must grant that the occurrence of the grandparental types in the offspring of hybrid parents in the ratio of three to one is no proof that the grandparents themselves differed in respect to one character alone, or that the difference between the two resulted from changes occurring at one time in the germinal constitution of an ancestor of one of them. Hence, in so far as this argument is concerned, there is in the case of *P. polytes*, for example, no assured reason for supposing that the *aristolochia*-like form did not attain its present appearance by a series of steps, of which a number of the later at least were preserved by virtue of the advantage they conferred upon the individuals in which they appeared.

[33] "Genetics and Eugenics," p. 188. Cambridge, Harvard University Press, 1916.

[34] Morgan, Sturtevant, Müller and Bridges, "The Mechanism of Mendelian Heredity," p. 164. New York, Henry Holt and Co., 1915.

[35] *Jour. of Genetics*, Vol. 5, pp. 37–50.

Little need be said regarding the inference that the constancy of the ratio in which the females of *P. polytes* seem to have occurred for many years shows that natural selection does not exist for this species in Ceylon, or else that its force is so slight that in half a century, and perhaps in a century and a half, it has produced no effect appreciable to the method of examination employed. This is valid only if it is true as postulated that the various types of *P. polytes* constitute "a population living and breeding together under the same conditions." But it is gravely to be doubted that this indispensable condition is fulfilled. We have some evidence (that of Bates and Wallace already cited) that butterflies which differ in color differ in habit, and if it should appear that the colors of butterflies in general are correlated with and repeat those of their surroundings, Punnett's fifth point is forever invalid. For it will be impossible to establish by observation the universal negative that is required, which is, of course, that the three types of female do not differ in any constant respect in their normal behavior.

Regarding the sixth point, which has reference chiefly to the fact of seasonal dimorphism among butterflies, it must first be affirmed that although the induced changes differentiating the broods of the spring and summer, or wet and dry seasons, are not directly inherited, the capability of responding definitely to the physical stimulus of changed temperature or humidity is a heritable racial trait.[36] The seasonal variations in the coloration of butterflies may be analogous upon the whole with the instantaneous color changes of tropical fishes, which also occur in response to external stimuli. The latter, however, follow more quickly than the former upon appropriate stimulation; they are reversible; and are known to be normally adaptive, since they reduce the conspicuousness of the individuals in which they appear. It may eventually prove to be a fact that instantaneous adaptive color adjustments, the phenomena of seasonal and sexual dimor-

[36] Professor Gerould first called attention to this fact in THE AMER. NAT., Vol. 50 (1916), pp. 310–316.

phism, and polymorphism all have the same biological significance, *i. e.*, that they represent different ways in which the coloration of a species exercises its obliterative function in a greater variety of circumstances than would be possible if it were uniform. Upon this view of the matter there would seem to be no reason why color variations of the seasonal sort should not provide material for evolution by natural selection.

Before suggesting another possible explanation of the fact of mimetic resemblance it seems desirable to state more specifically why certain of those already mentioned seem improbable.

Some color patterns are apparently limited to fishes whose habits are similar. Others occur which have survived the introduction of marked structural changes and are now the common property of whole families or groups of families, whose manner of living varies decidedly from species to species. There is one such system of coloring among grunts, groupers and snappers (Hæmulidæ, Epinephelinæ, and Lutianidæ), and Labrids and Scarids share another. In each pattern modifications may be noted which seem particularly appropriate under the local conditions in which they appear. Individual elements may lose all semblance of the original, and yet the nature of the whole be not obscured. But these facts make one skeptical regarding Thayer's hypothesis, for if, in butterflies too, detail is less important than the appropriate effect of the whole, the probability is remote that for different environments complex, ideal, protective or concealing patterns exist, whose slightest spot is so significant that there is marked tendency for forms of different racial endowment to attain them, if their habits are similar.

The same facts militate against such a conception as Packard's, that mimicry is a result of similar reaction to the direct influence of one set of external conditions. For coloration is characterized by such conservatism or inertia, and the same elements of pattern appear in such a variety of habitats, that the power of environmental in-

fluence to induce uniformity of coloration seems discredited.

If the possibility of the direct influence of local climatic factors be excluded, Piepers' hypothesis, that mimicry is largely due to species having independently attained the same stage of development orthogenetically, leaves the facts of geographical distribution of mimics and their models enshrouded in mystery. That this is a very real difficulty follows from Punnett's statement,[37]

> Examples of close resemblance between butterflies which live in different parts of the world are relatively rare and serve to emphasize the fact that the great bulk of these resemblance cases are associated in pairs or little groups.

Finally, instances of mimicry are, after all, only selected examples of resemblance, and it is desirable, if possible, to formulate an explanation that will apply to all equally well. But whether the likeness between them rises by sporting or otherwise, it is not to be supposed that Phasmids and green leaves or dry twigs possess Mendelian factors in common. Therefore it seems profitable to proceed for a little upon the assumption that mimicry is in some cases at least a visible token of the fact that the species manifesting it are linked by some bond other than common descent, common habit, or exposure to the influence of a common environment. What this may be, does not appear, unless through mutual resemblance advantage accrues to some or all of the forms concerned.

Evidence compiled by Marshall[38] shows that birds undoubtedly attack butterflies, but others deny that they feed upon the insects freely enough to affect the evolution of their coloration, and more particularly the mimetic resemblances between different species. Hence there is plainly a question at issue concerning the sufficiency of an assigned cause to produce a stated effect. Under the circumstances any evidence tending to show that the frequency of birds' attacks has been underestimated, or that

[37] *L. c.*, p. 54.

[38] *Trans. Ent. Soc. Lond.*, 1909, pp. 329–383.

their influence may be supplemented by that of other enemies is of the greatest interest.

In this connection Swynnerton's[39] observation that of twenty small bird excreta collected in the African forest no less than eighteen contained scales and small wing fragments of Lepidoptera has suggestive value. But, for the moment at least, it is more important that it appears that mimicry might be initiated and advanced by indiscriminate feeders, including lizards and insectivorous insects, provided only that they possess color vision. For to whatever extent such influence prevails it obviates the necessity of appeal to the effects of discriminate feeding by birds or other animals, and makes it possible to forestall the criticism to which reference has been made above.

Therefore it is suggested as a tentative explanation of mimicry, that it has commonly arisen as a result of bionomic pressure applied first by discriminate or indiscriminate feeders, which by elimination of unadapted variants have forced their accustomed prey to assume color combinations which most effectually conceal it in its normal environment. In addition, for no demonstrated reason, in a few of the many thousands of cases in which colors adapted to the environment and habits of their possessor have been evolved, patterns have appeared which have been sufficiently like one another to deceive enemies which exercise discrimination in their choice of food. Beyond this point the evolution of resemblance may have proceeded according to accepted formulæ, but without conspicuousness being involved at any point in the process.

It is submitted that in our present state of ignorance this construction may be placed upon observed facts rationally and without exposure to the criticism that has been directed against other attempted interpretations. However, the chief classes of facts to be explained and the most serious objections registered against the Neo-Darwinian hypotheses of mimicry will be presented, that

[39] *Ibis*, 1912.

the reader may judge whether a passage between Scylla and Charybdis may be made in safety.

Professor Poulton's extensive studies have convinced him that the evolution of mimetic resemblance has been directed by natural selection,[40] yet the evidence upon which his conclusion rests may be taken over bodily and supports the revised hypothesis as consistently as that to whose service it was originally dedicated. There is nothing anomalous in finding mimic and model living under the same conditions, certain groups of insects showing the same series of local color varieties, or such diversity of coloration appearing in one group of butterflies or moths as allies them outwardly with different "protected" genera. The same is true of the fact that insects with every variety of larval experience as adults possess the same type of coloration, that mimetic females are more common than males, or that the common coloration possessed by mimic and model is attained in the most diverse fashion, that is, that cases of mimicry are typical instances of analogy. Throughout the whole series of observations the points of agreement and difference are consistent, as far as is known, with the fundamental assumption that color and habit are associated variables.

Passing to the negative side of the argument, we may first consider the statement that it is impossible that reciprocal mimicry should have been brought about by natural selection of small variations. Punnett has this idea from Marshall[41] and uses it to emphasize the difficulty of the initial variation even in cases where it might seem that the theoretical advantage to be gained from mutual resemblance by two species would simplify the attainment of likeness. But Dixey,[42] against whose position the argument was originally directed, has exposed its unsoundness by calling attention to a number of critical

[40] See "Natural Selection the Cause of Mimetic Resemblance and Common Warning Colors" in "Essays on Evolution," 1908.

[41] *Trans. Ent. Soc. Lond.*, Vol. 45, pp. 93-142.

[42] *Trans. Ent. Soc. Lond.*, Vol. 45, pp. 559-583.

points which his opponent had failed to take into consideration.

It may be added that Marshall's reasoning rests upon what is without much doubt a baseless assumption, for he follows Müller in postulating that two species of distasteful insects will lose the same absolute number of individuals through attacks of ignorant enemies which in the beginning recognize neither of them. As a matter of fact, if two species differing in no respect except appearance are represented in the same area by 100,000 and 5,000 individuals, respectively, as Marshall assumes, the chances are 20:1 that any animal making an independent test of the food resources of its environment would first meet the more abundant form. Unless it learns its lesson perfectly from a single experience, the chances are essentially the same that it will kill another butterfly of the same kind before it encounters one of the second distasteful sort. But if most inexperienced enemies learn at the expense of one species that *some butterflies are not edible*, it is scarcely to be supposed that they will undergo as many unpleasant experiences before they retain an impression of the disagreeable character of the other. Hence Marshall's criticism can not be considered at present a valid objection.

Packard[43] believed that the concept of Müllerian mimicry had been overextended. He thought that in accumulating so many examples of warning coloration in their "Bionomics of South African Insects" Marshall and Poulton[44] in particular attempted to prove too much. Why an association of some scores of species representing many orders of Mashonaland insects should be pivoted upon the bitter-flavored beetle, *Lycus*, though some members of the group seemed more amply protected from attack by birds and lizards, was not clear. Yet one dares not be dogmatic in such matters, for the wasp, *Pompilus*, though more adequately equipped for defense than any other member of the association, may have drifted toward

[43] *Proc. Amer. Philos. Soc.*, Vol. 43, p. 424.

[44] *Trans. Ent. Soc. Lond.*, Vol. 41.

it at a comparatively late date, when the relatively slight distastefulness of a large number of insects of one type of coloration subtended a larger angle in the consciousness of insectivorous animals than the greater unpalatability of any single form. However, the idea that what has been considered mimicry is too common, and that in general the most effectively protected types should be the nuclei of the Müllerian combinations, is certainly not wholly unreasonable.

One of the chief reasons for believing in the existence of warning colors, and particularly of common warning colors, is the fact that some families of insects have slight range of color and pattern compared with others. Mayer[45] found that "the 200 species of *Papilio* in South America display 36 distinct colors, while the 450 species of Danaoid Heliconidæ exhibit only 15," and that "there is no lack of individual variability among the species of the latter, yet as a whole they vary but little from the two great types of color-pattern represented by *Melinæa* and *Ithomia*." To explain these facts he felt obliged to resort to Müller's hypothesis, but if instead of thinking of Ithomiinæ and Papilionidæ one considers Holocentridæ and Labridæ, an alternative solution appears. The squirrel fishes seem to be of red or reddish coloration the world over, but their habits are equally invariable, while the Labrids' diversity of coloring is no greater than that prevailing in the varied environments in which they live.

Such facts indicate the necessity of making detailed studies of the coloration of tropical Lepidoptera and correlating the facts discovered with the insects' distribution and behavior. When this is done there is reason to suppose that combinations of the same colors will be found upon animals of the same habit, which would have been as they are in many species, if any or all the others which display the same combinations had never existed. That is to say, it is probable that much that has masqueraded as Müllerian mimicry is nothing but the result of con-

[45] *Bull. Mus. Comp. Zool. Harv. Coll*, Feb., 1897, p. 225.

vergent evolution, which has been difficult to explain because of the deep-seated misconception that has prevailed regarding the function of animal coloration.

Dewar and Finn[46] cite a number of instances of resemblance between mammals, and others between birds, whose ranges coincide at no point. For the most part these likenesses do not seem comparable with the clearest cases of mimicry among insects in the degree of detailed resemblance they involve, and scarcely seem to rise above the level of interesting coincidences. It is unquestionably true, nevertheless, that such degree of likeness as may spring up between two species whose bionomic association is impossible on account of differences in geographical distribution, may also arise between species of one region without reference to the action of natural selection directed toward the production of resemblance.

Lock[47] states that Syrphid flies, which closely mimic small bees and wasps whose habits are similar to their own, are surprisingly numerous in southern Japan, and that their resemblance to bees is particularly noticeable, though these are conspicuous by their absence. Hence the question arises, how the flies can benefit by their resemblance to them: to which one must apparently answer, that under the conditions stated, the bee-like disguise can, as such, be of little value. But this query is overshadowed in interest by another: If the Syrphids are unprotected and driven by their enemies to assume the appearance of defended forms, how do they survive in regions where their disguise possesses no suggestion of unpalatability.

The idea is not to be entertained for a moment that Lock would be at a loss for an answer. But if the concept of warning coloration be abandoned, there is no reason to suppose bees less perfectly adapted in color and form than other animals to their respective modes of life. Bee-like flies whose habits resemble those of bees should there-

[46] "The Making of Species," pp. 242–245. London and New York, J. Lane, 1909.

[47] "Recent Progress in the Study of Variation, Heredity and Evolution," p. 58. London, John Murray, 1907.

fore be well able to exist beyond the range of models, which they may have mimicked in other times and places, if their particular type of coloration is as well suited to the new environment as to the old.

An apparent inconsistency in the Batesian and Müllerian hypotheses as at present interpreted has been frequently noted by hostile critics. To Reighard[48] it appears, for example, that if insectivorous vertebrates have pushed the resemblance between mimics and their models to the point of apparent identity, ordinary specific differences should suffice to warn them of the unpalatability of prospective and familiar prey.

This objection is so fairly met by the revised hypothesis, and the ground for criticism so completely removed, that further comment is unnecessary. But even when no inconsistency is involved in the explanation of the facts, some will doubtless consider the resemblance of the mimic to its model, or of insects to other objects, hypertelic. It is doubtful, however, whether hypertely embodies a real difficulty. For just as two streams flowing down a tolerably smooth inclined plane of infinite length will eventually unite, if all deviations of one or both which exceed a given magnitude are blocked when they tend to increase the distance between them, so, if heritable variations in the color and pattern of a given mimic are distributed according to Quetelet's law, for example, and only the extreme forms most unlike the model be eliminated in successive generations, closer and closer resemblance between the two may appear and approach identity without appeal to that over-refinement of vision whose existence among insects' enemies is at least problematical.

It is a standing objection to the mimicry hypotheses, and indeed to the explanation of any highly complex adaptation by natural selection, that at every stage the degree of resemblance attained must have been serviceable in order to assure its survival. It is understood, however, that this objection is applicable only to stages

[48] Carn. Inst. Wash., *Papers from Tortugas Lab.*, Vol. 2, p. 315.

following the first to which the selectionist ascribes deceptive value. Resemblance resulting from undirected variation, or existing for other reasons, is not subject to this criticism.

Darwin recognized this fact and attempted to throw upon another cause than natural selection a large part of the burden of producing functional resemblance. His idea may best be expressed in his own words:

> The process of imitation probably never commenced between forms widely dissimilar in color. But, starting with species already somewhat like each other, the closest resemblance, if beneficial, could readily be gained by the above means (natural selection), and if the imitated form was subsequently and gradually modified through any agency, the imitating form would be led along the same track, and thus be altered to almost any extent, so that it might ultimately assume an appearance or coloring wholly unlike that of the other members of the family to which it belonged. There is, however, some difficulty on this head, for it is necessary to suppose in some cases that ancient members belonging to several distinct groups, before they had diverged to the present extent, accidentally resembled a member of another and protected group in sufficient degree to afford some slight protection, this having given the basis for the subsequent acquisition of the most perfect resemblance.[49]

Weismann[50] attempted to avoid the same difficulty in another way. He makes no assumption that the original difference betwen mimic and model was distinctly less than that appearing at present between typical members of their respective families, but magnifies the importance of the first slight resemblance and subsequent positive variations. He had been deceived repeatedly, at least for the moment, by similarity in the flight of different species whose colors were not the same, and held as a consequence that mere variation in the manner of flight combined with the habit of associating with the form mimicked might have prepared the way for selection.

Wallace[51] would have it that certain butterflies, having

[49] "Origin of Species," Chap. XIV.

[50] "The Evolution Theory," Vol. 1, p. 93. London, Edward Arnold, 1904.

[51] "Darwinism," p. 243.

become unpalatable through the possession of disagreeable juices, developed distinguishing marks, whether in color, form or mode of flight. He then plunges *in medias res* with the assertion that "during the early stages of this process, some of the Pieridæ, inhabiting the same district, happened to be sufficiently like some of the Heliconidæ to be occasionally mistaken for them." Thereafter, as may be anticipated, evolution proceeded merrily, and examples of Batesian mimicry were perfected in due time.

Wallace's pronouncement begs the whole question. Weismann's hypothesis is conceivably true, but lacks the support necessary to carry conviction. Darwin's idea, finally, seems to be at variance with fact, since Poulton[52] infers from his own studies that the conclusion that emerges most clearly is the entire independence of zoological affinity exhibited by mimetic resemblance.

Punnett also shows most clearly how impossible the Darwinian suggestion is, but errs when he supposes that it can not be true in many cases that model and mimic were closely alike to start with. His demonstration may be accepted that the development of mimetic resemblance has not been commonly facilitated by preexisting likeness due to racial affinity, but he has wholly disregarded the fact that the degree of likeness which it is necessary to presuppose, if mimicry has been brought about by a series of comparatively small variations, might occur for other reasons.

May we not assume,[53] for example, that the Pieridæ and Heliconidæ are usually distinctly different in their habits, and that the coloration of typical members of each

[52] *Proc. Linn. Soc. Lond.*, Vol. 26, p. 570.

[53] This can scarcely be considered a rash assumption, since Wallace states (*Trans. Ent. Soc. Lond.*, Vol. 2, Ser. 2) that the Pieridæ of the Amazon valley generally are open-ground butterflies, two genera only, *Leptalis* and *Terias*, being true denizens of the forest. He also remarks that most of the species of *Heliconia* prefer the forest shades. It is also of interest to note that he comments upon the *inconspicuousness* of some species at least of *Ithomia*, in which connection one should recall the observation of W. J. Kaye already quoted.

group is a combination of hues well suited upon the average to render them inconspicuous in such places as they commonly frequent. If this be so, the initial step toward the production of new cases of mimicry might be any one of many variations in mode of nutrition or reproduction, which would lead representatives of the first family to spend their lives after the manner of the second. Reason has already been given for believing that convergence in color would probably accompany or follow convergence in habit.

The new colors would undoubtedly appear in patterns largely determined by and reflecting the Pierian ancestry. Among fishes, as has been stated, a primitive color pattern peculiar to one or common to several closely related families is sometimes readily recognizable, in which distinct elements are apparent, now definite, now diffuse, mere stains of dyes that are not permanent. It is to be expected no less in insects that the family patterns, like finely wrought ornaments cast into the melting-pot, will be reshapen and serve new purposes. But from the welter of change and recombination which this involves may come once in many times a new grouping of characters, which suggests the pattern of another race. At this point natural selection directed toward the production of a protective design painted in colors appropriate to the environment may yield to selection working in the direction of resemblance. If so, a new pattern may be developed in the same protective colors and coupled with such change in the shape of the wings, or in other characters, as confers the additional advantage of being mistaken for a species which enjoys some measure of immunity.

Either in organization or development most animals give evidence of changes in habit much greater than the initial one herein postulated. Yet admit that these may occur, and what is already partly proved, that color is correlated with habit throughout the animal kingdom, and a theoretical difficulty that has engaged the attention of adherents and opponents of the mimicry hypotheses van-

ishes. No matter how wide the original gap between mimic and model, it may be bridged; no matter what degree of similarity between two forms may be necessary before natural selection may become effective in heightening their resemblance, it may be attained without appeal to chance that is wholly blind, for there appears to be an automatic feature in the mechanism which has hitherto escaped observation.

The ideas outlined in the preceding pages are neither a pure product of reflection nor a compromise suggested by an examination of the literature upon mimicry. They are a normal outgrowth of studies which had no preconceived relation to the problem of mimetic resemblance. They constitute a working hypothesis, and as such are submitted to those biologists, particularly entomologists, who may have opportunity to test them rigorously.

NUCLEUS AND CYTOPLASM AS VEHICLES OF HEREDITY[1]

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THERE have been of late several attempts to effect a compromise between theories of heredity through the cytoplasm and theories which regard the chromosomes as the vehicles of inherited characters. Conklin ('08) was the first to suggest that egg, embryonic and general phyletic characters of any stage of the organism were determined in the egg cytoplasm while the determiners in the chromosomes made their presence known only through the specific or individual adult characters. Shull (1916) has elaborated this suggestion, and has brought to its support not only the older data on maternal inheritance, matrocline hybrids and the facts of development which relate to polarity, symmetry and organ-forming substances, but has added new evidence of his own from experiments with rotifers. Most recently, Loeb, in his book "The Organism as a Whole," has advanced a similar compromise theory, based on similar evidence.

Before examining in detail the experimental basis for such a compromise, it is important that the terms to be used be clearly and unmistakably defined. The first of these is the word "determined." That a character is determined in the germ cell means that the differential, causal antecedents of that character are present in the germ cell. It does not mean that the character itself is present in the germ in any form, but rather that it is represented by substances or forces which not only *stand for* the character but in some way bring about its expression.

[1] A review made at the suggestion of Dr. H. W. Rand to whom grateful acknowledgement is due.

If this definition of "determined" is accepted, two kinds of continuity in organisms are immediately differentiated. The first sort may be called *substantial* continuity. It is the carrying over from one generation to the next of autonomous organizations of protoplasm in a manner analogous to the carrying of the bacilli of certain diseases (*e. g.*, syphilis) in the germ cell. Here the germ cell is a passive vehicle. The character is present, not determined; and its changes from fertilized egg to adult are mere proliferations. If hereditary characters were to be so viewed, and the view carried to its logical conclusion, the result would be something very like an "emboitement" theory, which facts of development have proved to be untenable. Substantial continuity is hence only a concomitant rather than a part or a method of heredity.

The second type of continuity may be called "*genetic*" continuity, and characters which are genetically continuous are those which show a new coming into being with every generation. They are developed *anew*, and their resemblance to homologous characters in the preceding generation is due to their development not from *those characters* but from homologous determinants. Characters of this type are truly determined and all hereditary characters are reducible to this type whether they are exhibited in egg, sperm, embryo or adult.

It is now possible and desirable to define the expressions "inheritance through the cytoplasm" and "inheritance through the chromosomes." The first properly means that the locus of the determiners or representatives of a character is the cytoplasm, and since it is the egg alone which contains any significant amount of cytoplasm, the expression usually means the presence of these determiners in the egg cytoplasm. "Inheritance through the chromosomes" means that the chromatic substance of the nucleus is the locus of determiners, and since the nuclear content of egg and sperm is equivalent this must also mean an equal determinative share by egg and sperm in heredity.

Are now both of these theories compatible with one definition of "determined"? Are they both possible and both necessary?

Loeb has stated the problem and the "compromise" in these words (1916, p. 245):

> Question: "Is the organism nothing but a mosaic of hereditary characters determined essentially by definite elements in the chromosomes; and if this be true what makes a harmonious whole organism out of this kaleidoscopic assortment?"
>
> Answer: ". . . the cytoplasm of the egg is the future embryo in the rough, and the factors of heredity in the sperm only act by impressing the details on the rough block."

Shull's statement is as follows (p. 6):

> The cytoplasm often (perhaps usually) determines the type of cleavage, the early course of development, and in large measure the larval characters, while the adult characteristics are determined by the chromosomes.

Conklin's conclusions are (1915, p. 176):

> There is no doubt that most of the differentiations of the egg cytoplasm have arisen during the ovarian history of the egg and as a result of the interaction of nucleus and cytoplasm; but the fact remains that at the time of fertilization, the hereditary potencies of the two germ cells are not equal. All the early stages of development, including the polarity, symmetry, type of cleavage, and the pattern or relative position of future organs, being foreshadowed in the cytoplasm of the egg cell while only the differentiations of later development are influenced by the sperm. In short the egg cytoplasm fixes the general type of development and the sperm and egg nuclei supply only the details. We are vertebrates because our mothers were vertebrates and produced eggs of the vertebrate pattern—but the color of our skin, eyes and hair . . . were determined by the sperm as well as by the egg from which we came.

The same author has reiterated and somewhat elaborated the same views in an unpublished paper presented before the National Academy of Science in November, 1916.[1]

[1] Since the above was written Conklin's paper (1917) has been published. In its closing paragraphs he modifies materially the view which he had earlier expressed, admitting that cytoplasmic differentiation of the egg-cell probably arises under nuclear influence exerted equally by the egg and the sperm nuclei of the previous generation, the view maintained by the present writer.

The evidence and a criticism of parts of it follows:

1. Shull's Evidence

(*a*) Cases of maternal inheritance. Under this heading Shull places such experiments as those of Correns (1909) on *Mirabilis jalapa* var. *albomaculata*. This plant —the common four-o'clock—has variegated leaves, green and white, the white being due to inhibited development of green in the chromatophores. The amount of green and white varies in different plants and furthermore whole branches may be green while other whole branches may be white. Flowers borne upon green branches, if self-fertilized, give seed that produces only green offspring. Flowers from white branches, if selfed, give seed that produces only whites, which die because they are unable to carry on photosynthesis. Flowers on variegated branches yield offspring some of which are green, some variegated. Crosses among these green, white and variegated plants reveal the fact that the offspring resemble invariably the female parent. White females pollinated by any green or variegated pollen yield only whites which die. Green females pollinated by white or variegated pollen yield only green descendants. The paternal character never reappears in subsequent generations.

Correns has assumed in explaining these remarkable occurrences that a disease transmitted by the cytoplasm of the ovule is the cause of the color differences, inasmuch as the white color in either self condition or as mottling on the green is a pathological condition. The chromosomes are assumed to be immune to this disease. If the disease is caused by a germ (which is very likely) this germ acts only on the chromatophores and may well be passed through the egg like the germs of syphilis and other diseases. If this is the case, true heredity is not involved. The egg has simply acted as the passive bearer of a foreign body. And if the disease is due to a defect in the chromatophores, the case is not very different. The

chromatophores, as Shull says, are probably "autonomous bodies arising only from other autonomous bodies like themselves." On such a view they are simply structures enclosed within the cytoplasm, having a continuity parallel with but independent of the continuity of inherited characters.

(*b*) Shull's next evidence is drawn from experiments resulting in so-called "matrocline hybrids," which he defines as "unequal reciprocal hybrids which resemble the mother more than the father." Under this head he cites the well-known cases of species and genera crosses among echinoderms. He says of the first generation from sea-urchin ♀ × starfish ♂ (Loeb, 1903), and from sea-urchin ♀ × crinoid ♂ (Godlewski, 1906) that the embryos were purely maternal in character. In contrast to this, other observers of species and genera crosses among echinoderms (Morgan, Boveri, Baltzer and Herbst) have described the F_1 embryos as intermediate between the parents wherever there was normal union of maternal and paternal chromatin. Shull emphasizes especially the maternal character of embryos possessing no maternal chromatin. These were produced by Godlewski, by fertilizing enucleated fragments of sea-urchin eggs with crinoid sperm. The larval stages were reported to have been purely of the sea-urchin type. However, Boveri, Bierens de Haans and Herbst have obtained results which showed either the reverse condition, viz., *paternal* embryonic characters, or else intermediate larvæ. Moreover in the cross fertilization of giant sea-urchin eggs possessing twice the normal amounts of cytoplasm and chromatin, the larvæ inclined to the maternal side. That this was not due to the doubled amount of cytoplasm was demonstrated by Boveri, who fertilized *nucleated* half-fragments of normal eggs with sperm of another species and found no paternal inclination from the halved amount of cytoplasm. That the phenomena are due rather to the chromosomes is indicated by the same experimenter's work with dispermic fertilization. When more than one

sperm enters the egg abnormal mitotic figures and abnormal chromatin distribution are directly correlated with abnormalities in the larvæ, although the egg cytoplasm remains constant. Baltzer's fine work on species crosses may also be cited as showing that Loeb's and Godlewski's observations penetrated only part way toward the truth.

As an example, only one of Baltzer's crosses need be cited. When eggs of *Sphærechinus* were fertilized by sperm of *Strongylocentrotus*, the mitotic figures and distribution of chromatin were normal and the larvæ were intermediate, *not* maternal. From the reciprocal cross "matrocline hybrids" (most of them abnormal) did result, *but* their maternal resemblance was not due to cytoplasm. That it was due to irregularities in the chromatin distribution was proved by Baltzer, who followed the history of the maternal and paternal chromosomes in the hybrid embryos. He found that the majority of the paternal chromosomes (15 out of 18) were inactive at the first cleavage. They were extruded from the developing oösperm nucleus, and degenerated. The cells of the hybrid had then 21 chromosomes, 18 maternal and 3 paternal, and their maternal resemblance is easily explicable on these grounds. It is not explicable on any other for no abnormal conditions obtained in either cytoplasm or the surrounding medium.

Herbst repeated the first of Baltzer's crosses (*Sphærechinus* ♀ × *Strongylocentrotus* ♂) but chemically induced parthenogenetic development in the egg before the entrance of the sperm. Thus the ♂ pronucleus was behind at the first division and failed to be incorporated into the nucleus of one of the first daughter cells. One side of the developing hybrid had, then, merely paternal chromosomes, while the other had both maternal and paternal, and in striking sequence to this distribution were embryos which had only paternal characters on one side, while those of the other side were intermediate.

On the evidence thus far, Shull himself has not placed

the maximum of emphasis, and the foregoing criticism has been intended to indicate that its support of the cytoplasmic view has been and may continue to be so minimized as to be non-existent. However, Shull does place much emphasis on some carefully collected evidence of his own. This does not, I believe, support his theory to any greater extent than his quoted cases.

The evidence is briefly as follows: Shull crossed two lines of rotifers which differed in two egg characters—time of hatching of sexual eggs, and the proportions of sexual egs which actually hatched. The eggs of line "A" hatched on the average in 1–2 weeks, about 50 per cent. emerging. Line "B" eggs took 5–6 weeks to hatch and only 5 per cent. emerged. Line "A" females fertilized by line "B" sperm laid eggs which hatched in 1–3 weeks, 50 per cent. emerging. The eggs thus resembled the mother's line in both respects. Line "B" females fertilized by line "A" sperm laid eggs, 30 per cent. of which emerged in 4–5 weeks, resembling more the mother's line than the father's. The reciprocal hybrids are thus very unequal, says Shull, and since in crossing parents which differ by Mendelian, chromosome-determined characters, the resulting reciprocal hybrids are equal, the characters under observation are non-Mendelian and determined in the cytoplasm of the egg.

But it is to be objected that in reality these hybrid eggs of the first generation are not hybrid in these characters at all. The characters are egg characters and as such can be exhibited only when the hybrid zygote produces its eggs, not when the hybrid zygote is formed. The expression of the character is thus delayed until the hatching of eggs laid by these F_1 zygotes: And Shull's data shows this to be the case.

> But when new lines were obtained from these hybrid (F_1) eggs, and these lines produced sexual eggs of their own, the two reciprocal hybrid lines were *fully equal*.

Now the usual occurrence is observed, viz., the reciprocal hybrids are equal and the contributions to the character

by ♂ and ♀ are proved to be also equal. Shull's contention for the participation of the egg cytoplasm rests entirely on the maternal character of the first egg-generation. These eggs were matured, since the mother was homozygous in the characters, under the influence of the *like* chromatic contributions of her parents; the hybrid mother matured hers under the influence of the *unlike* chromatic contributions of her parents and showed the participation of her paternal chromosomes only in the *behavior* of her eggs. The peculiarities of the case lie not in that we are dealing with a cytoplasmically determined character, as Shull contends, but in (1) the fact that the characters are exhibited only by females; (2) in the fact that the characters are egg-characters, which places segregation one generation farther away from the original cross.

The case is quite analogous to the case of the inheritance of red pericarp color in corn, which, although a "maternal character," was shown to Mendelize by Lock ('06). It is also comparable to the egg-character "uni-bivoltinism" in silk moths, which Castle ('10) proved from Miss McCracken's data to be a Mendelian character. These cases will be discussed more fully in later paragraphs.

Shull's conclusion that cytoplasm determines egg and larval characters is, I believe, unnecessary. It has been shown that characters exhibited only by females and only in the egg may be equally determined both in the egg and in the sperm. The sperm contribution being predominantly chromatic, and the chromosomes being the accepted carriers of the determiners of other characters, it is to be concluded that the determiners for the characters investigated by Shull are also to be sought in the chromosomes.

Loeb, in his book (1916), has given considerable space to this question, closely following the earlier treatment by Conklin. His conclusion which has been stated and the evidence on which it rests may be briefly criticized by the

addition of further evidence which warrants a changed interpretation of certain facts.

Loeb first calls attention to the exclusively maternal character of the early development of enucleated fragments of eggs when fertilized by sperm of a different species. Such evidence has already been treated above (p. 5).

His second claim—that the *rate* of cell division and development is determined only by the egg cytoplasm—warrants further consideration. An egg from a line in which segmentation of the egg takes place eight hours after fertilization was fertilized by sperm from a line in which segmentation begins in 30 minutes. The rate of these cross-fertilized eggs was 8 hours, like the mother's line.

The careful and long continued work of Newman ('14) has, on the other hand, shown that the entrance of sperm of a different species does materially alter the rate of development.

> In both reciprocal crosses between *Fundulus heteroclitus* and *F. majalis* the rate of development of the hybrids was intermediate between that of the two parent species. This was true of cleavage rate, rate of germ-ring formation, etc.

In the cross *F. heteroclitus* $\times$ *F. diaphanus* "both reciprocal crosses have a higher rate than the pure bred strain. Similarly, when we make reciprocal crosses between *Cypronodon* and any species of *Fundulus* we find a marked retardation in developmental rate in both crosses. . . ." It is of the greatest significance that in all three cases the results of reciprocal crosses were equal. Either both were intermediate, both were accelerated or both were retarded regardless of which species was used as the egg-parent. In the face of such evidence, a theory of exclusive control of the egg over early development is untenable.

Newman's fundulus hybrids, while demonstrating the conclusion just stated, do not form critical evidence for determining the action in heredity of such rate-characters because only the F_1 generation is known. Another series

of experiments on a hatching time character has, however, been carried through the F_3 generation and as an illustration such a case may be cited in detail. It consists of Miss McCracken's (1909) experiments with silk moths. Castle later (1910) called attention to some facts in her data which indicated that although a female-exhibited character and confined to the egg in its expression, it nevertheless gave evidence of Mendelizing in crosses. Toyama ('12) concluded that dominance was present, and both of the latter investigators agreed that the males, although unable to exhibit the character, gave evidence by their genetic behavior of having an equal determinative influence with the females. The data follows:

Silk moths lay one batch of eggs, always in the spring. The eggs of some batches hatch out immediately, producing another brood of larvæ and moths in that season. The parents of such batches of eggs are hence known as bivoltins. The eggs of other batches do not hatch for twelve months, and since in this way there is but one brood or flight each season, the parents of such eggs are known as univoltins. If a univoltin female is crossed with a bivoltin male, the spring batch is laid as usual and hatches in 12 months. This is just what would have occurred if the mother had been fertilized by a male of her own sort. When these eggs hatch, a hybrid brood emerges which lay their egg batches immediately but the univoltin character is again exhibited in that all of these eggs are of the 12 months type. But, these eggs now differ among themselves as is shown by the behavior of the zygotes which emerge from them. Some of these females are bivoltin, laying eggs which develop immediately, while others are univoltin, laying eggs which hatch the following spring. The expression of the paternal contribution is delayed, but its activity in determining the time of hatching is quite apparent.

The inheritance of red pericarp color in corn follows exactly the same course as that outlined above, with red dominant over white. The F_2 embryos must be *raised*

before the segregation of pericarp color among them can be seen, for it is exhibited only in the seed coats. The conclusions follow: (1) The egg and all its determinative content is produced under the double influence of the sperm and egg chromatin contributions which united to form the producing zygote. (2) Hybridization experiments with egg characters, to be critical, must be carried as far the F_3 generation. (3) In all experiments which I have seen reported, in which this condition obtained, the influence of the sperm on the characters in question has been observed.

Loeb's evidence, however, introduces also crosses between *Strongylocentrotus purpuratus* and *S. franciscanus*, and the statement is made that the development of the hybrid up to the formation of the skeleton resembles exclusively the development of the mother's species. But Loeb also finds that the cross-barring in the spicules of *purpuratus* behaves as a dominant character in *reciprocal crosses*. He assigns this character to a factor, which he imagines to be a ferment or enzyme. This statement follows: "Since the pure *purpuratus* has two determiners for the development of the cross-bars, and the hybrids only one, the pure *purpuratus* should have twice the enzyme and develop twice as fast"—and it did. He provides here not only evidence that avowed chromosome characters do affect the *rate* of development, but even furnishes an enzymatic mechanism by which they may do it. And yet soon after the above quotation, we read:

> We can therefore be tolerably sure that wherever we deal with a hereditary factor which is determined by the egg alone, the cytoplasm of the latter is partly or exclusively responsible for the result. We have already mentioned that *rate of segmentation* is such a character.

The whole case of the supporters of any theory which views the cytoplasm as determinative rests on either their refusal to go back and inquire the source of this cytoplasm, or on their refusal to give due emphasis to the source, even though they recognize it. Conklin recognizes

the double influence which is exerted on the developing egg better than any of the others who have adopted his "compromise theory." He admits that "most of the differentiations of the cytoplasm have arisen during the ovarian history of the egg and as a result of the interaction of nucleus and cytoplasm." He has demonstrated better than any other one man how complex and definite these differentiations in the egg cytoplasm are. All will agree with him when he says that they "foreshadow" the future organism. But "cytoplasmic organization, while affording the immediate conditions of development, *is itself a result of the nature of the nuclear substance* which represents by its inherent composition the totality of heritable potence." These last are the words of E. B. Wilson (1895, p. 25), although he has translated and adapted them from an earlier paper by Driesch. They represent the opinion of Wilson and of Driesch in full accord. "The nuclear substance" referred to was even then known to contain equality of maternal and paternal chromatin.

Wilson himself had been able to demonstrate that the structure of the cytoplasm in sea-urchin eggs was acquired during ovarian life, and on the basis of this and of a considerable body of similar evidence he was able to conclude quite definitely:

> That a preorganization of the cytoplasm can not be regarded as the primary factor in heredity is conclusively proved by the old argument based on inheritance from the father through the sperm nucleus.

The only link which is needed to make the chain complete is some substantial body of evidence, demonstrating the effect and the mechanism of action of the nucleus on the cytoplasm. This, it must be admitted, has not been entirely filled. Nägeli, to be sure, held a theory of a dynamic effect of the nuclear idioplasm on the cytoplasm, while Driesch contended that the mechanism was chemical. The nucleus, in his opinion, exercised its governance by means of ferments or enzymes. There are facts in

development which point to effects of the nucleus even on the visible differentiation of the egg before fertilization. In the sea-urchin, for instance, this differentiation is preceded by the absorption into the nucleus of part of the fluid content of the cytoplasm, altering the chemical composition of the latter and greatly increasing the bulk of the nucleus. The membrane of this enlarged nucleus then dissolves and part of its contents by their color may be traced to a clear cap of fluid which later gives rise to the skeleton of the echinoderm. Such absorptions and minglings probably play a large part in the reactions of nucleus and cytoplasm, either at the successive disappearances of the nuclear membrane during mitosis or through that membrane.

Nucleus and cytoplasm may certainly be regarded as forming a reaction system analogous to that which might exist between a series of chemical substances (Jennings, 1914). The cytoplasm in turn is linked with the extracellular milieu in a quite comparable way and forms the intermediary between the nucleus and the exterior.

Evidence on this interaction is accumulating. As an example I may quote the work of Cameron and Gladstone on cells other than ovarian, and, to be sure, by the static, histological method. But they have observed fine preparations and have concluded that the cytoplasm is visibly differentiated into two grades of endoplasm. The first is next to the nucleus, is clear and refractive. This is the nascent material of the cell and is the first visible stage in the genesis of protoplasm. It is, they postulate, a derivative of the nucleus itself, and to the nucleus is ascribed the final elaboration of nutritive material which has been ingested by the cytoplasm. This nascent endoplasm they conceive to be the active material of the cell grading into passivity toward the cell periphery, through the maturer endoplasm and the ectoplasm.

Whatever relations may exist between the two, the fact remains that the cytoplasm is necessary. Without it the nucleus, deprived of its milieu, can not live, and develop-

ment can not take place. The investigation of the finer physiological reactions which take place between the nucleus and cytoplasm is badly needed, and the restatement of them in terms of physics and chemistry. Such evidence as is available indicates that the importance of the cytoplasm is, in the main, subordinate to that of the nucleus.

The evidence from egg-characters, it might be noted in conclusion, is one-sided. I have no doubt that if sperm-characters were to be studied as intensively as egg-characters have been (which has not been the case due to the microscopic size of most sperms) the differential characters in the sperm would be found to behave in heredity like the differential characters of eggs, and would be determined as largely by the egg nucleus as by the nucleus of the sperm of the preceding generation.

Conclusions

Direct continuity of substances in the cytoplasm is not a method of heredity. It simply provides for the autonomous proliferation of materials with no determinative significance. No compromise, then, is possible between the two views outlined as "cytoplasmic" and "chromosome" theories of heredity. The first is non determinative; the second is the primarily effective method of heredity and of development. The working of the effective method is known for heredity, if heredity be properly only concerned with the way in which the hereditary factors are distributed in the germ cells. For development, its mechanism is but grossly known, but we have learned enough of the determinative effect of the nucleus and of the possibilities for interaction between cytoplasm and nucleus to foster a suspicion that one day the governance of the chromosomes over development will be explained in physical-chemical terms.

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SHORTER ARTICLES AND DISCUSSION

MODIFYING FACTORS AND MULTIPLE ALLELOMORPHS IN RELATION TO THE RESULTS OF SELECTION

In the prevailing controversy as to the effectiveness of selection, those who reject such effectiveness put forth *multiple modifying factors* as the explanation of the results observed. The given character (for example, the coat color in Castle's hooded rats) is held to depend on one main factor (determining the presence or absence of the character) and upon numerous modifying factors; the number of the latter present in a given case determines the degree of expression of the character. Selective breeding is then held to act, as it does with relation to all other Mendelian factors, merely by making diverse combinations of such factors. Many are gathered together in certain individuals, few in others, and the degree of expression of the inherited character varies accordingly.

Much evidence is presented that this is actually the mode of operation in many cases where selection is effective. Thus are explained the visible results of selection in Castle's rats; thus the unexpected fact that many of the mutations of *Drosophila* have shown themselves (in accordance with Castle's prediction) to be amenable to selection, although in other respects they behave like alterations of a single unit factor. This is indeed the usual explanation for that effectiveness of selection which is coming to light in so many cases; and in many of the cases it appears clear that the explanation is correct.

But in which direction does this explanation carry us? To answer this question we must know what these multiple modifying factors are. If they are mere examples of the static condition of diversity observed among so many closely related organisms, the answer falls in the negative direction, so far as the effectiveness of selection in accumulating actual alterations of hereditary characters is concerned. But if they should themselves turn out to be the actual alterations of hereditary constitution that are accumulated by selection, then the answer con-

firms the effectiveness of selection and adds greatly to our knowledge of how it is brought about. What are the facts?

For these we may turn to the organism of which the genetics are best known; to the fruit fly *Drosophila;* and we may accept the accounts presented by those most uncompromising opponents of the effectiveness of selection, the investigators of *Drosophila* in the Columbia laboratory. Their account we cannot suspect of being colored to favor the selectionist point of view. We find data as to certain known modifying factors in the recent important paper of Bridges (1916) on "Non-Disjunction of the Chromosomes in *Drosophila.*" Bridges tells us that he has found no less than seven diverse factors that modify the single primary grade of eye color known as eosin. These seven factors are located in parts of the chromosomal apparatus different from the spot on which the presence or absence of eosin depends, and each is inherited in Mendelian fashion. One of these factors lightens the eosin color in a fly with eosin eyes, nearly or quite turning eosin to white; this factor Bridges calls "whiting." Another has the effect of lightening the eosin color a little less, giving a sort of cream color; this is called "cream *b.*" A third factor dilutes the eosin color not so much; it is called "cream *a.*" In addition to these, Bridges tells us that he has discovered three other diluters of the eosin color; we will call them the fourth, fifth and sixth diluters. And finally Bridges tells us of another factor whose only effect is to make eosin darker; this factor he calls "dark." We get therefore the following list of the modifying factors for eosin color:

1. Whiting
2. Cream *b*
3. Cream *a*
4. Fourth diluter
5. Fifth diluter
6. Sixth diluter
7. Dark

We have then in *Drosophila* minutely differing conditions of a single shade of color, brought about by seven modifying factors. Concerning these, Bridges makes the following remark, which is worthy of particular attention:

A remarkably close imitation of such a multiple factor case as that of Castle's hooded rats could be concocted with the chief gene eosin

for reduced color, and these six diluters which by themselves produce no effect, but which carry the color of eosin through every dilution stage from the dark yellowish pink of the eosin female to pure white (Bridges, 1916, p. 149).

Thus we see that in *Drosophila* we could get the same sort of graded results that Castle does with his rats, only in *Drosophila* this is by multiple modifying factors, whereas Castle believes that in the rat it is by actual alterations in the hereditary constitution!

But what are these modifying factors? And here we come to the astonishing point. *These modifying factors are themselves alterations in the hereditary constitution!* Bridges leaves no doubt upon this point. He lists and describes them specifically as mutations; as actual changes in the hereditary constitution.

Now so far as I can see, the question involved in the selection controversy is as to the occurrence of minute changes in the hereditary constitution, and their accumulation by selection; so that by selection various grades of a given external character can be obtained. In *Drosophila*, according to Bridges, such changes occur; changes which give, so far as our present imperfect knowledge goes, at least seven diverse grades of a single tint (that is itself, as we shall note, only one grade in another series of seven known grades). By means of these graded changes one could obtain, by the mutationist's own statement, the continuously graded visible results which selection actually gives. Is not then the controversy as to the effectiveness of selection at an end?

As to just where the graded hereditary changes occur there remain indeed certain differences of opinion; some selectionists, like Castle, hold that the various grades of a given external character are due to diverse minute modifications of the same unit character—of the same locus in the chromosome; while, as we have seen, the modifying factors are due to changes in diverse parts of the hereditary material. This matter of detail does not touch the main point, but it is of interest to ask what the work of the mutationists gives us on this question. It is curious to find that their studies of *Drosophila* furnish almost all that could be asked by the radical selectionist as to the existence of a single unit character in a series of numerous hereditary gradations. The best instance here is again the color of the eye, which furnished us also our example of modifying factors. The color

eosin, of which the modifying factors give us seven grades, is itself only one of another series of seven grades that are due to diverse alterations in the same unit factor—in the same chromosomal locus. As we know from the studies of *Drosophila*, this locus is a certain region of the X-chromosome. When this locus retains its normal condition the eye is red. Some years ago a variation was observed by which the eye lost its red color, becoming white. Somewhat later another variation came, by which the eye color became eosin. By the wonderfully ingenious methods which the advanced state of knowledge of the genetics of *Drosophila* has made possible, it was determined that the mutations white and eosin are due to changes in a particular part of a particular chromosome, and that indeed the two are due to different conditions of a particular region of the X-chromosome. In other words, they show different conditions of the same unit. Moreover the normal red represents a third condition of this same unit.

Later a fourth condition of this same unit was found, giving a color which lies nearer the red, between the red and eosin; this new color was called cherry. We have now four grades of this single unit character.

And now, with the minute attention paid to the grades of eye color, new grades begin to come fast. In the November number of *Genetics*, Hyde (1916) adds two new grades, one called "blood," near the extreme red end of the series; the other, called "tinged," near the extreme white end; in fact, from the descriptions, it requires careful examination to distinguish these two from red and white respectively. So we have now six grades of this unit. And in the same number of the same journal, Safir (1916) adds another intermediate grade, lying between tinged and eosin; this he calls "buff."

So, up to date we know from the mutationists' own studies of *Drosophila* that a single unit factor presents seven gradations of color from white to red, each grade heritable in the usual Mendelian manner. These grades or "multiple allelomorphs" as they are called, are the following:

1. Red
2. Blood
3. Cherry
4. Eosin

5. Buff
6. Tinged
7. White

Three of these seven grades have been made known to us within the last six months. It would not require a bold prophet to predict that as the years pass we shall come to know more of these gradations, till all detectable differences of shade have been made out and each shown to be inherited as a Mendelian unit. Considering that the work on *Drosophila* has been in progress but eight or nine years, we have already remarkable progress toward a demonstration that a single unit character may present as many heritable grades as can be distinguished; that the grades may give a pragmatically continuous series. This is precisely the situation that the selectionist postulates.

Furthermore, as we have seen, besides this primary series of seven grades, due to alterations of a single unit factor, there is a secondary series containing seven more grades, all affecting the central grade (eosin) of this primary series, but due to alterations of other parts of the germinal material. How much more does the selectionist require?

This situation in *Drosophila* is not exceptional. To mention one or two other examples, Castle and Wright (1916) find a large series of such diverse conditions of a single factor ("multiple allelomorphs") determining various shades of coat colors in rodents. Emerson (1917) in his recent account of the extraordinary condition of affairs in the genetics of pericarp colors in corn, talks of "a series of not less than nine or ten multiple allelomorphs," which moreover leap back and forth from one condition to another in bewildering fashion.

To sum up, it appears to me that the work in Mendelism, and particularly the work on *Drosophila,* is supplying a complete foundation for evolution through the accumulation by selection of minute gradations. We have got far away from the old notion that hereditary changes consist only in the dropping out of complete units, or that they are bound to occur in large steps. The "multiple allelomorphs" show that a single unit factor may exist in a great number of grades; the "multiple modifying factors" show that a visible character may be modified in the finest gradations by alterations in diverse parts of the germinal material. The objections raised by the mutationists to gradual change through selection are breaking down as a result of the thoroughness of the mutationists' own studies.

The positive contribution of these matters to the selection problem is to enable us to see the important rôle played by Mendelism in the effectiveness of selection. Hereditary variations, such as give rise to the multiple allelomorphs and multiple modifying factors, occur in some organisms rather infrequently, as measured by the time scale of human happenings. If there were no interchange of factors among individuals and stocks, it would take a long time to obtain in one individual all the six diluters of the eosin color of the *Drosophila* eye; one arises in one individual, another in another. But by selective crossbreeding it is possible to bring together into one stock all the modifiers that have been produced in diverse stocks. Mendelism acts as a tremendous accelerator to the effectiveness of selection.

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A WING MUTATION IN PIOPHILA CASEI

IN the early part of December, 1915, I began to breed the "cheese skipper" *Piophila casei*, in order to see if mutations were to be found in this fly. The source of my stock was a small piece of Italian cheese containing a dozen or so larvæ.[1] As these were doubtless the offspring of one female, inbreeding has been very close. Up to June 22, 1916, only one heritable mutation had been found among the thousands of individuals bred; this was the wing defect described below, which was first noted on March 12, 1916.

[1] This work was carried on at the Osborn Zoological Laboratory, Yale University, New Haven, Connecticut. It was in New Haven that I obtained the cheese. Contribution No. 135, Zoological Laboratory, University of Texas.

The Defect.—When viewed from the dorsal surface the defect appeared as a blister of variable size on the proximal and posterior part of the wing. From the ventral surface it appeared as a pit. Occasionally a real blister filled with fluid was obtained. The position of the defect was constant; when small it lay in the posterior cell just below the discal cell. When large it involved nearly the whole wing including the axillary, anal, second basal, discal and posterior cells. Usually both wings were affected alike, but here and there flies were found with one wing normal and the other wing severely affected.

This factor is strikingly similar, both in its appearance and the variability of its behavior, to the "balloon wings" found by Morgan[2] in *Drosophila* and more recently fully described by Marshall and Muller.[3] The flies carrying the defect, in my cultures, were very frequently sterile, and in no case did their fertility begin to approach that of normal stock.

In breeding, the character behaved as a mendelian recessive. Normal crossed with balloon gave, in the F_1 generation, 196 normal and no affected individuals. (This included 4 matings.) When brother and sister were mated, in the F_2 generation, 312 normal and 111 balloon offspring were obtained This is very close to the expected 3:1 ratio, of a monohybrid cross. When balloon flies were crossed, all individuals were affected (74 offspring obtained) but the character showed itself extremely variable; in some cases the flies appeared normal until very closely examined.

The defect was not sex-linked as is shown by the following mating. A defective female was mated with a normal male of normal stock. Of the 50 offspring resulting both males and females were normal.

The variation in the appearance of the balloon flies suggested either that the size of the blister was dependent upon some unknown environmental factors, or else, was due to multiple allelomorphs or multiple factors. A great number of matings were made to gain light on this point, but due to the sterility of the affected individuals, the evidence is not sufficient to allow us to draw any conclusions. Two individuals both of whom were severely affected were crossed. The 20 offspring resulting were all severely affected. Two individuals, both of whom were only

[2] In Morgan's "A Critique of the Theory of Evolution."

[3] Marshall and Muller, *Jour. of Exp. Zool.*, Vol. 22, 1917.

slightly affected, were crossed. Of the 29 offspring resulting, 17 showed the defect in a severe form, and 12 showed only small blisters. A female which had only one wing affected, was mated to a male, one of whose wings was severely affected while the other bore a very small blister. Of the 45 offspring resulting, 27 bore the defect in a severe form on both wings and 18 showed small blisters again on both wings.

Further experiments with this new character were under way when the work was stopped by the mobilization of the Militia in June. The work with these flies, however, is again being resumed.

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A CASE OF REGENERATION IN PANULIRUS ARGUS[1]

THE occurrence of regenerative processes in the crustacea has been a matter of record for a number of years, but the instances have been mostly confined to the regeneration of appendages and portions of the nervous system. Observations on the regeneration of portions of the exoskeleton of the trunk are far less numerous. The present observations on the regeneration of a portion of the rostrum of *Panulirus argus*, the common crayfish of the Bermuda Islands, were made during the summer of 1916 at the Bermuda Biological Station.

Panulirus argus when full grown is about 14 to 16 inches in length. It lacks chelipeds, their place being taken by the ordinary type of walking appendage. None of the walking appendages is provided with nippers, all being tipped with a single hook, as, *e. g.*, in the fourth pair of appendages of the crayfish *Cambarus*. The rostrum of *Panulirus*, instead of being a single median projection, consists of a pair of long (30–35 mm.), sharply pointed spines, slightly compressed laterally, and growing out from the carapace just posterior and slightly dorsal to the base of the eye-stalks.

The animal in question was a half-grown male, eight and one half inches long. When caught, June 20, the left spine (compare figure and explanation) of the rostrum was entirely missing. The carapace around the base was jagged and rough, as though the break had been recent; but a thin, soft membrane had

[1] Contributions from the Bermuda Biological Station for Research, No. 58.

formed across the surface of the break. Five days later, June 25, the protecting membrane had hardened, so that it could not be dented with the point of a scalpel. No further change could be noted until after the molting, which occurred four days later, June 29. The casting occurred at night, and the next morning the new shell showed no signs of any wound. By one o'clock a very slight hump appeared, and by ten o'clock at night a little rudimentary spine 2 mm. in length had formed. The next morning another millimeter had been added to its length. Meantime the normal spine had increased 1.5 mm. in length. No further growth followed before the new shell had hardened.

FIG. 1. From a photograph of the left side of the head region of *Panulirus argus*, showing (*norm.*) the normal, and (*regn.*) the regenerated rostral spine. As the figure is reproduced from a photographic print, the picture is reversed, the right spine appearing like a left one.

Sixteen days later, July 15, another molt occurred. As before, the old shell was cast at night and by the following morning the regenerating spine had added 2 mm. to its length, being now 5 mm. long. By the next evening all growth had been stopped by the hardening of the new shell, but the total length of the spine was at this time 7 mm. The spine now showed a sharp point and also a slight lateral compression like that of the normal spine. At this casting the normal right spine added 1 mm. to its length, showing that, while the whole animal was growing, the

regenerating part was increasing at a much faster rate than other parts.

Thus in the period of twenty-seven days during which the animal was under observation, it had undergone two molts and had regenerated a missing rostral spine of normal form, 7 mm. in length, while the normal spine had added 2.5 mm. to its length in the same period. These results show that the period between molts for this animal under laboratory conditions is sixteen days; that a rostral spine of normal form can be regenerated; and that the rate of this regeneration was nearly three times the rate of normal growth of a similar spine during the same period.

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NOTES AND LITERATURE

THE COAL MEASURES AMPHIBIA OF NORTH AMERICA[1]

THE excellent monograph by Dr. Roy L. Moodie is a worthy successor of the long series of works by Dawson and by Cope on the air-breathing vertebrates of the Coal Period in North America. The extremely varied amphibian fauna of the coal swamps as described by Moodie contains representatives of no less than 7 orders, 19 families, 46 genera and 88 species, the animals ranging in size from the minute *Eumicrerpeton*, less than two inches long, to the great *Leptophractus obsoletus*, which was as large as an adult Florida alligator. The wide differentiation and high specialization of these amphibians shows that the class even at that early epoch had evolved very far from its first adaptive radiation, so that, as Dr. Moodie well observes, the origin of land vertebrates from fishes must be looked for in a much earlier time, perhaps the Silurian.

Carboniferous Amphibia are reported from various localities in North America, but only four of these have yielded large or important collections. From the South Joggins coal mines in Nova Scotia Sir William Dawson secured most of the specimens of Microsaurs described by him, many of the skeletons being found in the rotten stumps of *Sigillaria* trees. This material is preserved chiefly in the Museum at McGill University, Montreal. From the Linton, Ohio, coal seams Newberry and his collectors secured the great collections described by Cope and which are now chiefly in the American Museum of Natural History. At Mazon Creek, Illinois, the fossils are found in ironstone nodules in a stratum of shale; the specimens have been described chiefly by Newberry, Cope and Moodie and are scattered in various museums. At Cannelton, Pennsylvania, the fossils occur in slates and have been described by Moodie, the material being in the National Museum.

On account of the fragmentary nature of most of the material and the fact that generic and specific names have been based on

[1] Carnegie Institution of Washington, Publication No. 238, 1916.

many different and non-comparable parts of these animals, the author's task was an exceedingly difficult one, and only those who have occasion to study this work very closely can appreciate either the magnitude of the undertaking or the thoroughness with which it has been carried out.

Dr. Moodie's monograph will naturally invite comparison with the well-known works on the Permian Amphibia of Bohemia and Saxony by Fritsch and by Credner. It must be admitted, however, that many of the illustrations are inferior to those of the works mentioned, partly on account of the difficulty of showing the real character of these fragmentary specimens by means of photographs.

The author's method is so intensive that he has left even readers who may have some first-hand knowledge of Paleozoic Amphibia in need of many broader facts and comparisons which may reasonably be expected to result from such a conscientiously executed investigation; it is the aim of this review in some measure to supply this deficiency, in the hope that Dr. Moodie himself may be induced to write a general article covering more fully the points here raised.

In the chapter on stratigraphic and geographic distribution the author shows that the four chief Amphibia-bearing formations in North America mentioned above are all in the Alleghany or Lower Coal Measures and are thus much older than those deposits (Salt Fork, Pitcairn) of the Upper Productive Coal Measures at the top of the Pennsylvanian series, which have collectively yielded *Cricotus, Diplocaulus, Eryops* and other genera characteristic of the Texas "Permian."

The author does not discuss the faunistic relations of the Lower Coal Measures fauna either with the "Permian" fauna of Texas and other states, or with the Carboniferous and Permian faunas of Ireland, Scotland, England, France, Saxony and Bohemia. Even the Permian and Triassic amphibian faunas of South Africa invite comparison with the varied Temnospondyli of the Carboniferous and Permian of America and Europe.

The Lower Coal Measures fauna of America includes a long series of branchiosaurs, microsaurs and primitive labyrinthodonts (*Spondylerpeton, Dendrepeton, Macrerpeton, Eobaphetes*), and it is totally lacking in pelycosaurs, poliosaurs, cotylosaurs, or any other reptiles except *Eosauravus*. The Texas fauna, on the other hand, has only a single microsaur (*Crossotelos*) and no branchiosaurs; its varied labyrinthodonts

(including *Cricotus, Eryops, Dissorophus* and many others) are all genera not found in the Lower Coal Measures, and it abounds in reptiles of several orders and many families. Some of this difference may be due to the fact that the Lower Coal Measures fauna represents only the life of the coal swamps, while the Texas fauna represents the life of the pools and streams of a wide delta country (Case); but all authorities agree that the former is much the older of the two.

The Lower Coal Measures fauna is far more similar to the Permian fauna of Bohemia, which according to Fritsch's classification comprises a similar series of 13 families, 26 genera and 63 species, of branchiosaurs, microsaurs and temnospondyls. But no genera are common to the two countries and many of the "families" (as listed) are peculiar to one or the other. The families peculiar to America are the Cocyctinidæ, Peleontidæ, Tutidanidæ, Ptyoniidæ, Molgophiidæ, Sauropleuridæ, Amphibamidæ, Ichthycanthidæ, Stegopidæ, Macrepetidæ, while those peculiar to Europe are the Apateonidæ, Limnerpetidæ, Microbrachidæ, *Dolichosoma, Ophiderpeton,* Melosauridæ and Archegosauridæ. The families common to both continents are: Branchiosauridæ, Diplocaulidæ,[2] Hylonomidæ, Urocordylidæ, Nyraniidæ,[3] Cricotidæ (Diplovertebridæ), Anthracosauridæ, Mastodonsauridæ.

Professor Case has directed attention[4] to the marked resemblance of two of the genera (*Diplovertebron, Macromerion*) from the lowest Bohemian horizon (Nyran) to *Cricotus* of the Upper Coal Measures of North America, as furnishing evidence that the Bohemian deposits are of Upper Carboniferous age.

Subsequent research may well show on the one hand that some of the American "families" are more closely related to European groups than is now recognized and on the other hand that some of the "families" classed as common to both continents are artificial or ill defined (Hylonomidæ?, Nyraniidæ?); yet even with our present imperfect knowledge it appears that the Lower Coal Measures fauna of America and the "Permian" fauna of Europe represent nearly identical life conditions and similar

[2] *Brachyderpeton* of the English Coal Measures, as shown by Watson, appears to be related to *Diplocaulus*.

[3] The presence of this family in America is doubtful, and Dr. Moodie's reasons for assigning the genera *Ichthyerpeton* and *Cercariomorphus* to this family are not stated and difficult to infer.

[4] *Science*, Vol. 42 (Dec. 3, 1915), pp. 797–798.

adaptations on the part of two divergent associations derived from some older and common source, possibly of Mississippian age and of wide distribution; and it further appears probable that the American Lower Coal Measures fauna is somewhat the older of the two.

The chapter on the morphology of the Coal Measures Amphibia contains a careful description of the characters of the skull and other parts of the skeleton, but the author is extremely chary of generalizations. He might have mentioned, for instance, the interesting fact that the skull-pattern of these amphibians is a shifting mosaic, one in which several of the dermal elements have different contacts and different positions in the various families. In some microsaurs, for example, the postorbital grows backward and secures a broad contact with the tabular; in others it retains its primitive position. The jugal and lacrymal also differ widely in their form and contacts. The nasals and adjacent elements are small and much crowded in many branchiosaurs and microsaurs, long and wide in most labyrinthodonts. Certain dermal elements are present in some and absent in others, especially the intertemporal and the rare interfrontal and internasal elements. The shape of the occiput differs widely, sometimes truncate posteriorly, with the auditory notch obsolete, sometimes angulate posteriorly, retaining the primitively wide auditory notch. Very curious is the tendency of the different families of microsaurs to develop "horns"—sharp backwardly projected apophyses in the occipital region—growing sometimes from the tabular, sometimes from the squamosal and sometimes from both at once. These remind one of the backwardly directed processes from the "epiotic" and supraoccipital in the skull of teleost fishes and perhaps they may have served for the attachment of longitudinal ligaments or muscles in wriggling, aquatic types.

All the differences in skull pattern may be regarded as minor readjustments which were taking place after the more profound transformation of a generalized pro-ganoid skull into the amphibian type, the greatest alteration including the loss of the opercular bones so as to leave the gill chamber covered only by membrane and the change of the preoperculars or cheek plates into the squamosals. The author expresses the opinion that the membrane bones may have originally been derived from scales "which later became consolidated into large bony scutes," but on histological grounds the reviewer regards it as far more prob-

able that in the ancestral fishes each membrane bone and each scale grew from clusters of cosmine tubercles underlain by tracts of vascular and stratified bony tissue, and that there never was a time when the elements of the dermo-cranium were scale-like in form (*i. e.*, rhombic or polygonal), although the several tissues involved were histologically identical in the body scales and in the dermo-cranium.

On page 85 the author uses the name "squamosal" for the element which he and most other authorities now designate as "supratemporal."

In the description of the hyobranchial elements of *Coccytinus* (a genus doubtfully assigned to the Proteida), the reader looks in vain for a comparison with the same elements in the Permian "Urodele" *Lysorophus* as described by Williston. It may be noted, by the way, that the branchial arches in that genus are extremely primitive and almost *Polypterus*-like in form and arrangement, although doubtless homologous also with those of the modern *Amblystoma*.

The author has given a very thorough study of the dermal scales and scutes of the branchiosaurs, microsaurs and temnospondyls. The ventral "scutellæ," which appear to be homologous with the abdominal ribs of reptiles, are formed, the author holds, as ossifications in the connective-tissue septa or myocomata of the ventral muscles, vestiges of these having been found in modern urodeles. The highly differentiated characteristics of this ventral armature affords many family and generic characters; it is sometimes absent or reduced to needle-like ossicles, sometimes highly developed, forming heavy median V's and wide lateral shelves (*Ctenerpeton*). Some of the microsaurs had rounded, slightly imbricating fish-like body scales with concentric markings which recall the similar armature of certain Bohemian and Saxon types, such as *Ricnodon* and *Discosaurus*. Vestiges of such conditions may be represented in the scales of modern cæcilians (as shown in the enlarged figures of cæcilian scales by the Sarasin brothers).

The reviewer ventures to doubt the correctness of Dr. Moodie's reconstruction of the shoulder-girdle of branchiosaurs and microsaurs, in the matter of the position of the scapula. Many of the specimens figured by Fritsch and by Credner seem to indicate that the concave border of the scapula was posterior in position, as it is in *Eryops* and in modern urodeles, and that it did not form the glenoid border as in Dr. Moodie's reconstructions.

Dr. Moodie's history of the classification of the Amphibia appears to the reviewer to be rather meager, since he simply lists the classifications of his predecessors without giving any critical discussion. It is surprising that in this chapter he did not mention the work of Fritsch with which he must be extremely familiar. Fritsch's classification of the extinct Amphibia, although it was adapted and extended from the classification proposed by the British Association Committee in 1870, was, in the judgment of the reviewer, a distinct contribution to the subject which certainly deserves notice in an historical review, especially since Fritsch erected several new families and gave definitions of all the European groups.

The author's own classification is an interesting attempt to divide the Amphibia of the Coal Measures into two major series or subclasses, the first (Euamphibia) including all those which may be related to modern types; the second comprising all the wholly extinct groups (microsaurs, aistopods and labyrinthodonts of all suborders). He derives most of the modern urodeles (Caudata) from the branchiosaurs, for which he has given considerable evidence; he follows Cope in provisionally deriving the modern Proteida from the Cocytinidæ of the Coal Measures. He regards the strange *Diplocaulus*, an amphibian with a head like a colonial cocked hat, as a member of the Euamphibia, probably because its vertebræ bear short, straight, double-headed ribs which are attached to paired lateral apophyses springing from the middle of the vertebræ, after the fashion of those of branchiosaurs and Caudata and quite unlike the hour-glass centra of microsaurs, which bear long, slender ribs between the vertebræ. But Watson and Williston regard *Diplocaulus* and *Brachyderpeton* as microsaurs, the last named genus showing in the vertebræ and in the skull how the *Diplocaulus* type may have been derived from primitive microsaurian conditions. Indeed it may well be argued that the branchiosaurs and urodeles (Caudata) themselves, in spite of the retention of gills in the young, may have been derived from primitive microsaurs, that is that the vertebræ and ribs of microsaurs are on the whole much more primitive than those of branchiosaurs and Caudata.

The systematic relations and origin of the frogs and toads remain doubtful. Dr. Moodie gives an excellent discussion of the resemblances of *Pelion lyelli* Wyman, from the Linton, Ohio, Coal Measures, to the modern Anura but leaves the phylogenetic problem open. *Pelion* is so little known that it may or not be

ancestral to the Anura, and the Jurassic Anura are so entirely modernized that they do not bridge over the wide structural gap between the Paleozoic Amphibia and the modern frogs and toads. It seems to the reviewer, after repeated comparisons of the osteology of the Anura with that of many of the temnospondyls, that some members of the latter group, in the brain-case, the dermo-cranium and even in the vertebræ and limbs retain many characters which may reasonably be looked for in Paleozoic ancestors of the frogs and toads; and that such forms as *Brachyops*, *Cacops* and *Dissorophus*, although not directly ancestral, differ from the Anura chiefly in the retention of many primitive amphibian characters. It may be that some of the short-headed Triassic temnospondyls of South Africa will furnish the linking forms; but at any rate it is interesting to note that the existing frogs and toads retain a long series of characters in the skull and skeleton which are seen in the Paleozoic temnospondyls, and that they differ from the latter in such modernized characters as the following: the wide fenestration of the occiput and palate, the resulting slenderness of the skull bones, the loss of the dermo-supraoccipitals, tabulars, ectopterygoids, pre- and post-frontals, the completion of the auditory ring, the development of extreme saltatorial adaptations in the skeleton, including the modification of the vertebræ from the rhachitomous into the notocentrous and epichordal types, the development of a long continuous urostyle coincident with the forward shifting of the sacrum and lengthening of the ilium.

Dr. Moodie's arrangement and sequence of the families of microsaurs appear to the reviewer to be highly confusing. It would perhaps have been better, after beginning with the newt-like types, to pass at once to the long-bodied Urocordylidæ and the snake-like Molgophiidæ and Ptyoniidæ, instead of interjecting in the middle of the series the Stegopidæ, which appear to the reviewer to be more nearly allied with the Temnospondyli, and the Amphibamidæ, which are heavy-limbed offshoots of the primitive microsaurs.

The author's ordinal and family definitions are extremely full, but the reader will find so many characters that are common to several families and sometimes orders, that it is difficult to cull out the most striking ones. This the reviewer has attempted to do in the subjoined table in which he has also included the principal European families of branchiosaurs and microsaurs. The families of microsaurs are arranged so far as pos-

sible in the general order of their specialization, proceeding from the more primitive newt-like forms to the snake-like microsaurs or Aistopoda.

SYNOPSIS OF THE PRINCIPAL BRANCHIOSAURS AND MICROSAURS OF AMERICA AND EUROPE

A. Vertebræ phyllospondylous, *i. e.*, having the notochord expanded in the middle of each vertebra; transverse process in dorsal region large; ribs short, straight and heavy and borne on the transverse processes, usually near the middle of the vertebræ. Skull broad, obtusely rounded.

B. Auditory notch posterior rather than lateral in position. *Branchiosauridæ.*

BB. Auditory notch extended laterally, the squamosals lying far forward .... *Apateonidæ.*[5]

AA. Vertebræ lepospondylous, *i. e.*, with the centra forming gently constricted cylinders; ribs intercentral, typically long and curved.

B. Digits (when present) 4 in manus, 5 in pes; carpus and tarsus cartilaginous. . .

C. Body newt-like.

D. Body covered with cycloid scales or sculptured scutes. Hind limbs longer than fore limbs.

E. Skull narrow .... *Hylonomidæ.*

EE. Skull broad.

F. Ribs short, slightly curved. *Limnerpetidæ.*[5]

FF. Ribs thin, curved ...... *Microbrachidæ.*[5]

DD. Body-scales reduced or absent; neural and hæmal spines of caudal vertebræ often expanded.

E. Ventral scutellæ absent, tail moderate in length, skull without "horns." *Tutidanidæ.*

EE. Ventral scutellæ weak or moderately developed, tail long.

F. "Horns" on squamosals. *Diceratosaurus.*

FF. "Horns" on tabulars. *Urocordylidæ.* *Brachiderpeton.*[6] *Keraterpeton.*[6]

EEE. Ventral armature highly developed, consisting of rods, plates or stout bristles. Skull (so far as known) without "horns." Ribs broad and heavy. Limbs well developed with claw-like phalanges .... *Sauropleuridæ.*

F. Skull very wide and obtuse; teeth heterodont .... *Saurerpeton.*

[5] Permian of Europe.

[6] Europe.

FF. Skull moderately elongate; teeth homodont. *Sauropleura*.

FFF. Skull very large; teeth with acute compressed apex and anterior cutting edge. *Leptophractus*.

FFFF. Skull unknown; abdominal ribs very heavy with broad shelf-like lateral extensions; spines of vertebræ pectinate as in *Urocordylus, Œstocephalus* and *Ptyonius*. *Ctenerpeton*.

CC. Body *Proteus*-like (serpentine). Limbs much reduced or absent .... (*Aistopoda*).

D. Ventral armature weak or absent.

E. Ribs long, heavy and broad; neural and hæmal spines short or absent .... *Molgophiidæ*.

EE. Ribs delicate, single-headed; neural arches wide with low spines. Skull narrow, pointed. *Dolichosoma*.[7]

EEE. Ribs well developed; neural and hæmal spines of caudals expanded, pectinated; skull lanceolate with long, slender teeth ... *Ptyoniidæ*.

DD. Ventral armature consisting of narrow, oat-shaped scutellæ; ribs forked, two-headed; neural arches with low spines, lower transverse process expanded into a wide plate in the anterior half of the vertebra. Skull shorter and blunter than in *Dolichosoma*. *Ophiderpeton*.[7]

CCC. Body stout; limbs well developed (but still with cartilaginous carpus and tarsus). Tail short, head very large. Ribs long.

D. No "horns" on squamosal, skin covered with rounded or hexagonal tuberculated scales. Ventral scutellæ present .... *Amphibamidæ*.

DD. Squamosals produced into "horns." Ventral scutellæ apparently similar to those of *Amphibamus*. *Eoserpeton tenuicorne*.[8]

BB. Digits of manus unknown; pes with well ossified tarsus. (Limb suggests *Erypos*). Ventral scutellæ delicate. Centra amphicœlous, spines broad and heavy .... *Ichthycanthidæ*.

AAA. Vertebral centra discoidal.

B. Vertebræ short, thick and probably amphicœlous. Body covered with small cycloid scales .... "*Nyraniidæ*" (?).[9]

C. Body newt-like .... *Ichthyerpeton bradleyi*. *Cercariomorphus*.

[7] Europe.

[8] Placed by Dr. Moodie in the Urocordylidæ, but possibly related to *Amphibamus*.

[9] The skull of *Nyrania* as figured by Fritsch (Vol. II, p. 34) appears to the reviewer to relate this genius with the Temnospondyli; but it is placed provisionally by Dr. Moodie in the Microsauria.

CC. Body *Proteus*-like ....*Ichthyerpeton squamosum.*

BB. Vertebræ checker-like, deeply amphicœlous. .*Eosaurus.*

AAAA. Vertebræ unknown. Skull of pretty generalized type with separate intertemporal. Lacrymal and nasals large, orbits central rather than anterior; squamosals produced into short, divaricate "horns." ....*Stegopidæ.* (*Stegops*).[10]

[10] May be remotely related to the Temnospondyli (W. K. G.).

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